The eyes of *Tegula funebralis* may represent a concentration of the same sensitive tissue present on the general body normally outside of the shell. The pigmentation of the retina resembles that of the epidermis, which contains melanin. Attempts to isolate a photosensitive pigment from the eyes, according to the recipe for squid retinas (Bliss, 1948) failed, probably because of the very small amount of tissue employed.


## SUMMARY

*Tegula funebralis* is negatively phototactic. It becomes adapted to bright light, and loses its sensitivity temporarily. It has a general body sensitivity shown by a shadow reaction. Its eyes, simple lens ocelli, seem responsible for directional orientation to light. Without eyes its orientation is irregular.


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# Observations on the Epipodium, Digestive Tract, Coelomic Derivatives and Nervous System of the Trochid Gastropod *Tegula funebralis*


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(15 Text figures)

In spite of the abundance of *Tegula funebralis* (A. Adams, 1854) in the California intertidal, no account of its anatomy has yet appeared in the literature, although the anatomy of other trochids has been described (Randles, 1905; Fretter and Graham, 1962). To partially fill this void, a brief account of certain external and internal features of *T. funebralis* is herein presented.

The specimens of *Tegula funebralis* examined were collected at Mussel Point, Pacific Grove, California, during April and May, 1963. The animals were dissected alive after having been anesthetized with magnesium chloride; both frozen and paraffin sections were cut in order to make more detailed observations. Injection of suspensions of carborundum and carmine powders in sea water helped to determine the extent of specific body cavities. Both Mallory's connective tissue stain and Harris' hematoxylin produced excellent results after fixation with Bouin's fluid, made with seawater. A silver impregnation (Rowell, 1963) worked well for isolated nerves, but also stained muscle and connective tissue heavily in sections of the entire animal.

**Epipodium:** The epipodium of *Tegula funebralis* is composed of five elements: the neck lobes, anterior papillæ, epipodial tentacles, epipodial papillae, and epipodial ridges (Figures 1 and 2). On both sides of the animal the anterior quarter of the epipodium is occupied by the heavily ciliated neck lobe, which runs posteriorly from near the base of the optic peduncle. The border of

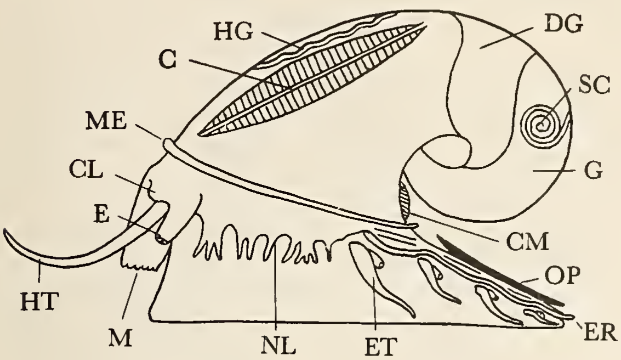


Figure 1: Entire animal, left side, shell removed

| | |
|---|---|
| C ctenidium | G gonad |
| CL cephalic lappet | HG hypobranchial gland |
| CM columellar muscle | HT cephalic tentacle |
| DG digestive gland | M mouth |
| E eye | ME mantle edge |
| ER epipodial ridge | NL neck lobe |
| ET epipodial tentacle | OP operculum |
| SC spiral caecum | |

the left neck lobe is fringed, the number and grouping of points being variable, whereas the edge of the right lobe is smooth; on both lobes the cilia beat distally, especially when the lobe is touched with a probe. The function of

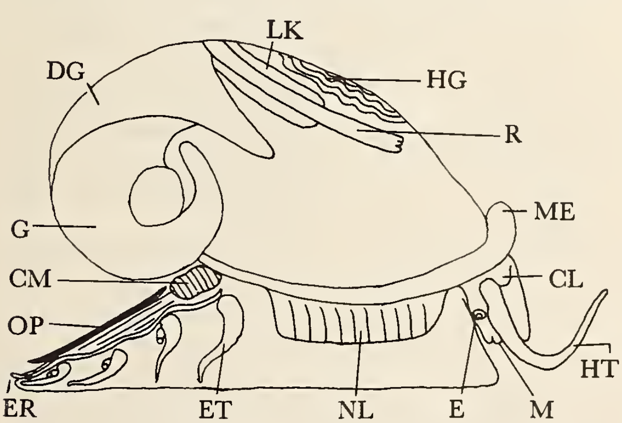


Figure 2: Entire animal, right side, shell removed.

| | |
|---|---|
| CL cephalic lappet | HT cephalic tentacle |
| CM columellar muscle | LK left kidney |
| E eye | M mouth |
| ER epipodial ridge | ME mantle edge |
| ET epipodial tentacle | NL neck lobe |
| G gonad | OP operculum |
| HG hypobranchial gland | R rectum |

these neck lobes may be the removal of particles expelled from the mantle cavity, though Fretter & Graham (1962, p. 532) state that the neck lobes of British trochids are rolled into half-siphons for channeling water in and out of the mantle cavity. No evidence of this was seen in *Tegula funebralis*.

Beneath the overhang of each neck lobe are from one to ten anterior papillæ, each with a central spot of ciliated unpigmented epithelium (Fig. 3). They retract slightly when touched; this reaction and their structure suggest that they may be sensory receptors.

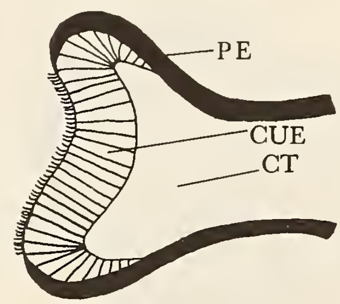


Figure 3: Anterior papilla, diagrammatic longitudinal section

| | |
|---|---|
| CT connective tissue | CUE ciliated unpigmented epithelium |
| PE pigmented epithelium | |

Just posterior to the neck lobe is the first epipodial tentacle, which on the left side bears an epipodial papilla (Fig. 6) similar in appearance to an anterior papilla; the first epipodial tentacle on the right side does not bear such a papilla. The other three tentacles on each side bear papillæ (Fig. 4). The epipodial tentacles are similar in structure to the cephalic tentacles and are innervated from the pedal cords; observations of the use of both cephalic and epipodial tentacles in the field and in aqua-

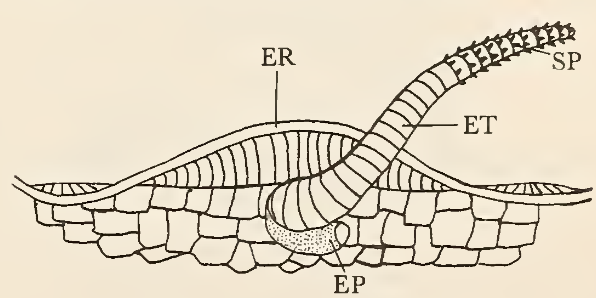


Figure 4: Epipodial tentacle, diagrammatic

| | |
|---|---|
| EP epipodial papilla | ET epipodial tentacle |
| ER epipodial ridge | SP sensory papillae |

ria seem to indicate that they are tactile, and perhaps olfactory, receptors. An active animal will be seen to draw its tentacles repeatedly over the substrate as it advances. Resting animals either "caress" their shells with the tentacles, or gently wave them. In the presence of predaceous asteroids such as *Pisaster ochraceus* (Brandt, 1835), *T. funebralis* waves cephalic and epipodial tentacles vigorously while trying to escape; Mc Gee (unpubl.) has noted a similar response in *Tegula brunnea* (Philippi, 1848) exposed to spawning males of their own species.

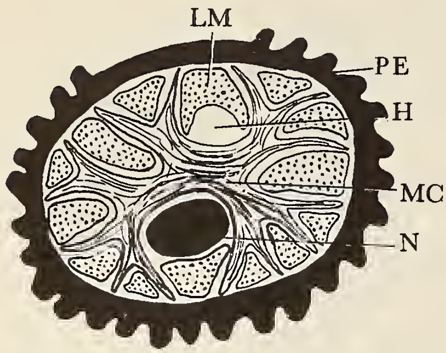


Figure 5: Epipodial tentacle, diagrammatic cross section

H haemocoel
LM longitudinal muscle band
N nerve
MC column of transverse muscle and connective tissue
PE pigmented epithelium

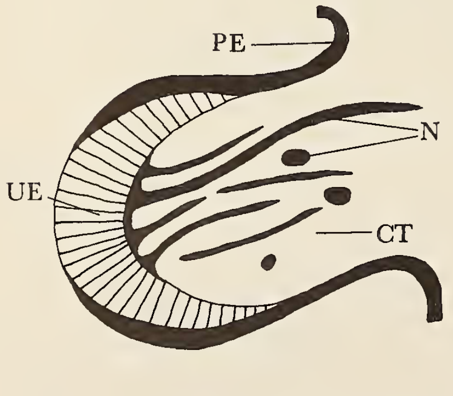


Figure 6: Epipodial papilla, diagrammatic longitudinal section

CT connective tissue
N nerve
PE pigmented epithelium
UE unpigmented epithelium

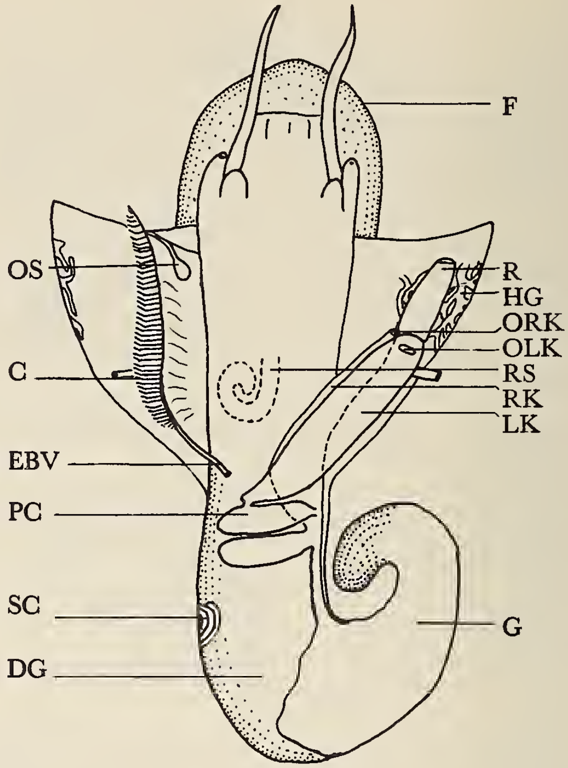


Figure 7: Dorsal view of entire animal with mantle cavity laid open; structures of coelomic origin are indicated

C ctenidium
DG digestive gland
EBV efferent branchial vein
F foot
G gonad
HG hypobranchial gland
LK left kidney
OLK left kidney opening
ORK right kidney opening
OS osphradium
PC pericardium
R rectum
RK right kidney
RS radular sac
SC spiral caecum

The epithelium of the epipodial tentacles is heavily pigmented; distally it forms papillæ bearing non-motile sensory cilia. Similar cilia are found on the tentacles of other prosobranchs (Fretter & Graham, 1962, p. 313) and on the oral tentacles of the nudibranch *Hermissenda* (Agersborg, 1925). Passing down the length of the tentacle is a large central nerve, longitudinal muscle bands, and an extension of the hemocoel. The center of the tentacle is occupied by an irregular column of muscle and connective tissue fibers (Fig. 5). The epipodial ridge is a long flap of tissue which begins just posterior to the first epipodial tentacle on either side and runs just dorsal to the other three epipodial tentacles and continues to the hindmost tip of the foot.

**Digestive Tract:** The anterior part of the digestive system seen in Figure 8, shows the buccal cavity to be limited ventrally by the subradular membrane, which extends posteriorly into the radular sac. Ventrally, the radular sac is anchored by striated musculature to the posterior part of the odontophore. The radula is fused to the subradular membrane anteriorly, but is free posteriorly. The complex movements of the odontophore are controlled by striated musculature acting on the four radular "cartilages."

The disposition of the rest of the digestive system is seen in outline in Figure 9. There are three main regions: the foregut, composed of buccal cavity and esophagus; the stomach and digestive gland, which comprise the midgut region; and the hindgut, consisting of intestine and rectum. Only one duct is shown leading to the digestive gland from the stomach; there are also numerous fine pores in the same area which appear to lead to the gland. The areas of the posterior visceral hump occupied by the digestive gland and gonad vary somewhat from specimen to specimen. In freshly killed specimens which were not treated with magnesium chloride, peristaltic movements could be seen in the hindgut, but were not observed in the foregut.

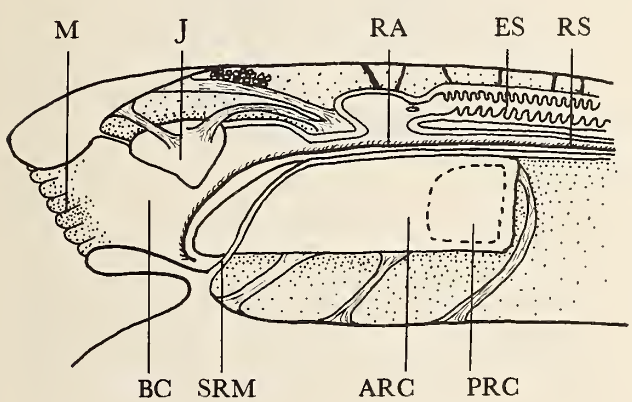


Figure 8: Buccal region, diagrammatic longitudinal section

ARC anterior radular cartilage
BC buccal cavity
ES esophagus
J jaw
M mouth
PRC posterior radular cartilage
RA radula
RS radular sac
SRM subradular membrane

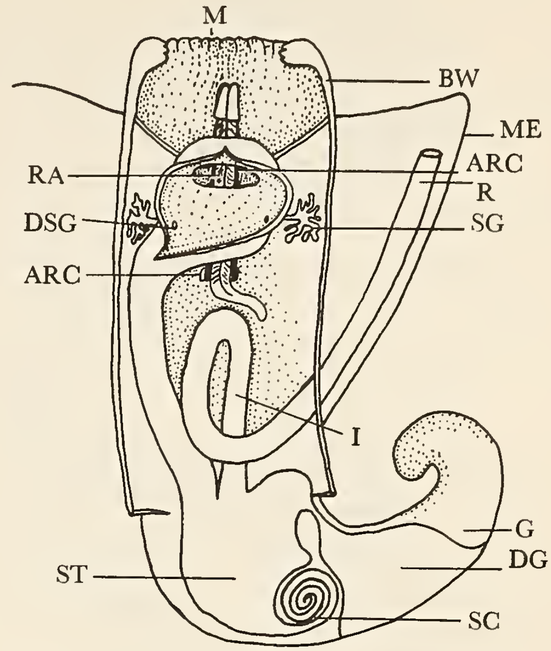


Figure 9: Dorsal view of entire digestive system

ARC anterior radular cartilage
BW cut edge of body wall
DG digestive gland
DSG duct of salivary gland
G gonad
R rectum
I intestine
M mouth
ME mantle edge
RA radula
SC spiral caecum
SG salivary gland
ST stomach

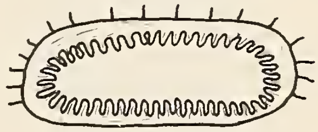

Figure 10: Cross section through esophagus

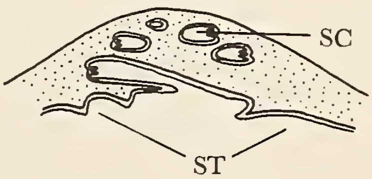


Figure 11: Cross section through spiral caecum

SC spiral caecum
ST stomach


Figure 12: Cross section through rectum

CA cilia CT connective tissue

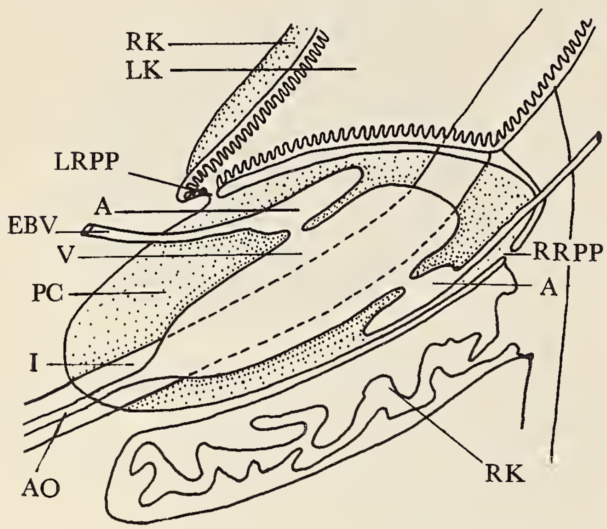


Figure 13: Diagrammatic dorsal view of pericardial cavity showing coelomic derivatives

A auricle
AO aorta
EBV efferent branchial vein
I intestine
LK left kidney
PC pericardium
RK right kidney
RRPP right renopericardial pore
LRPP left renopericardial pore
V ventricle

**Coelomic Derivatives:** Structures of cœlomic origin are shown in figure 13; these include the right and left kidneys, the pericardial cavity, and the gonad. The presence of both right and left renopericardial ducts is in accord with the condition found in other trochids (Randles, 1905) and in *Haliotis* (Harrison, 1961). The duct to the right kidney is very small; whether it is functional or not is undetermined. The opening to the left kidney is relatively large, and fluid may be caused to flow between the left kidney and the pericardial space.

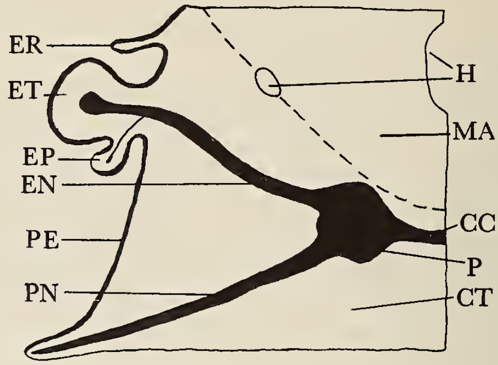


Figure 14: Left side of foot, diagrammatic cross section

CC cross connection between pedal cords
CT connective tissue
EN epipodial nerve
EP epipodial papilla
ER epipodial ridge
ET epipodial tentacle
H haemocoel
MA muscular area
P pedal cord
PE pigmented epithelium
PN pedal nerve

**Nervous System:** The nervous system of *Tegula funebralis* (Figs. 14 & 15) is similar to that of other trochids (Randles, 1905, pp. 57-66, figs. 30-33). The right pleuro-parietal connective runs over the esophagus and splits into two nerves, the first running to the branchial ganglion, subjacent to the osphradium, and the second running posteriorly between the ventral ctenidial membrane and the perivisceral sinus, and crossing the esophagus and the loop of the hindgut to end in a pair of visceral ganglia above the right kidney. The left pleuro-visceral connective crosses beneath the esophagus and runs posteriorly to connect with the visceral ganglia. Randles (1905) found a dialyneury between the left pallial nerve and the right pleuro-parietal connective in *Trochus;* no such connection was observed in *Tegula funebralis.*

## ACKNOWLEDGMENTS

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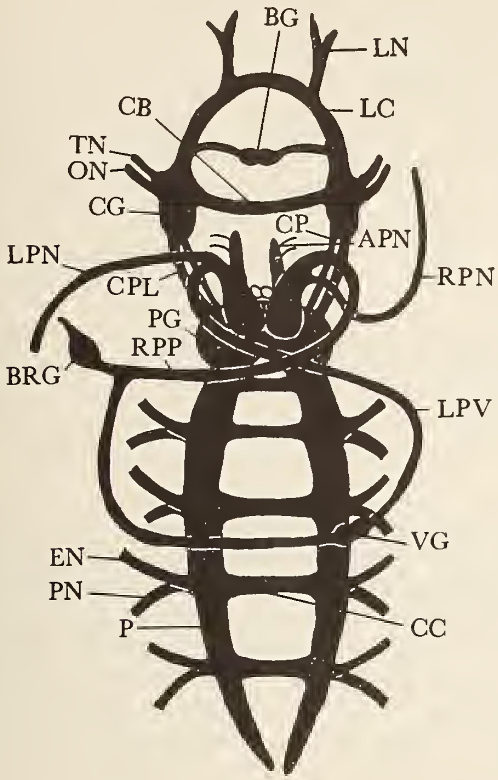


Figure 15: Nervous system, diagrammatic dorsal view. The large masses dorsal to the pedal ganglia represent the pleural ganglia; the small hollow objects between the pleural ganglia are the statocysts

APN anterior pedal nerve
BG buccal ganglion
BRG branchial ganglion
CB cerebral commissure
CC cross connection between pedal cords
CG cerebral ganglion
CP cerebro-pedal connective
CPL cerebro-pleural connective
EN epipodial nerve
LC labial commissure
LN labial nerve
LPN left pallial nerve
LPV left pleuro-visceral connective
ON optic nerve
P pedal cord
PG pedal ganglion
PN pedal nerve
RPN right pallial nerve
RPP right pleuro-parietal connective
TN tentacle nerve
VG visceral ganglia

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